# THE WESTERN AMERICAN SPECIES OF PAEONIA

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In all recent treatments of the genus *Paeonia* in the western United States, only one species has been recognized, *P. Brownii* Dougl. The range of this "species," however, is most unusual. *Paeonia* occurs commonly in cismontane southern California at low altitudes. It is rare in central California, but reappears as a frequent or common plant at medium altitudes, in the northern part of the North Coast Ranges and in the northern Sierra Nevada, and from there extends northward to British Columbia and eastward to Wyoming.

Struck by this remarkable discontinuity in range, several systematists have maintained that the peony of southern and south central California is specifically distinct from that of the northwest. Nuttall, whose manuscript description is quoted by Torrey and Gray (8), described the southern form as *Paeonia californica,* which, he stated could be distinguished from the northern *P. Brownii* by its "smaller, less divided leaves, which are deep green on both sides, and the leaflets bifid or trifid, never pinnatifid," as well as by possessing three rather than five carpels. Nuttall's type of *P. californica* was collected near Santa Barbara; Douglas' type of *P. Brownii* in Oregon, "near the confines of perpetual snow on the alpine range of Mt. Hood." Unfortunately, additional material of both species revealed that, with the exception of green rather than glaucous leaves, all of the characteristics mentioned by Nuttall occur also in the northern *P. Brownii.* Many plants of this species have leaves smaller than those of typical *P. californica;* in some specimens of *P. Brownii* the leaves are not more dissected than are those of the southern plant; the number of carpels varies from two to five in both. Probably recognizing these facts, Gray (2) as well as Brewer and Watson (1) considered *P. californica* a synonym of *P. Brownii.* The authors of recent California floras, Jepson (4, p. 373) and Munz (6, p. 170) have also recognized only *P. Brownii,* and have not even mentioned *P. californica* as a synonym.

The strongest case for recognizing *Paeonia californica* as a distinct species was presented by E. L. Greene (3). He drew a graphic picture of the ecological differences separating the two but failed to give any valid diagnostic characters to distinguish between them, except leaf color and shape of leaf segments. Using these characteristics, Lynch (5) recognized *P. californica* as a variety of *P. Brownii.*

The writer became interested in this species problem through cytological and systematic studies of the Old World species of the genus. Upon examining herbarium specimens, it was found that after a little study one could tell almost at a glance, without looking at the label, whether a specimen was from southern California

Table 1.—Comparison of *Paeonia Brownii* and *P. californica*

| | *P. Brownii* | *P. californica* |
|---|---|---|
| Habit | | |
| Number of flowering stems per plant | 1–16 | 5–30 |
| Height of flowering stems | 2–4 dm. | 3.5–7.5 dm. |
| Number of leaves per stem | 5–8 (av. 6–7) | 7–12 (av. 9–10) |
| Character of branching | stems usually simple, sometimes with 1 or 2 short branches | stems always branched or with rudiments of branches in axils of upper leaves; in luxuriant plants the larger primary branches bear secondary branches |
| Cataphylls | | |
| Apex | obtuse | acute |
| Leaves | | |
| Color | glaucous | green |
| Texture | thick, usually somewhat fleshy | thin, easily wilting |
| Base of primary segments | abruptly contracted, petiolulate | cuneate, sessile or with short, alate petiolules |
| Terminal secondary segment of middle cauline leaf, length | 3.5–6.0 cm. | 2.8–7.5 cm. |
| Terminal secondary segment of middle cauline leaf, width | 2.5–5.5 cm. | 1.1–4.5 cm. |
| Ratio of length to width | 0.8–1.4 | 1.5–3.0 |
| Number of ultimate lobes on terminal primary segment of middle cauline leaf | 13–44 | 10–17 |
| Shape of ultimate lobes | elliptic, usually obtuse | lanceolate or narrowly elliptic, usually acute |
| Flowers | | |
| Petals | rotund to orbicular | elliptic |
| Length of largest petal | 8–13 mm. (av. 9–11) | 15–25 mm. (av. 19–21) |
| Width of largest petal | 10–15 mm. | 11–18 mm. |
| Ratio of length to width | 0.7–1.0 | 1.1–1.6 |
| Petal, color of center | maroon or bronze | deep blackish red |
| Petal, color of margin | yellowish or greenish | pink (sometimes a narrow yellowish margin at the apex) |
| Length of longest filaments | 4.2–5.5 mm. | 6.0–8.5 mm. |
| Length of longest anthers | 3.3–5 mm. | 3.5–7 mm. |

or from the north. The exact differences between the two, however, were not easily defined, largely because the leaves of *Paeonia* are rarely well spread out in the preparation of speci-

mens, the bulky flowers are usually crushed in such a manner that little can be told of their fresh condition, and there are rarely enough flowers on a specimen to permit dissection.

For this reason, the writer has paid particular attention to *Paeonia* on collecting trips. Several collections of *P. Brownii* were made during the seasons of 1936 and 1937 in Nevada, Sierra, Lassen, and Shasta counties in northeastern California, and a small colony was discovered on the northeast side of Mount Hamilton, Santa Clara County, in the Coast Range. This is a southerly extension of the known range of typical *P. Brownii;* the nearest known locality to the northward is in Lake County, about 150 miles distant by air line. The southern plant was studied and collected in 1937 at the type locality near Santa Barbara, as well as near San Luis Obispo and at the foot of Cajon Pass, San Bernardino County; in 1938 its most northerly known locality, Pine Canyon, west of King City, Monterey County, was visited. In making each collection, a number of flowers were dissected before pressing as described elsewhere (Stebbins, 7).

On the basis of these observations, the existence of a number of real distinctions between *P. Brownii* and *P. californica* was established. These are stated in Table 1 and the most important summarized in the following key:

Stems 2–4 dm. high, bearing 5–8 leaves; leaves more or less glaucous, their primary divisions abruptly contracted at the base to distinct, often elongate petiolules, the ultimate lobes elliptic; petals rotund or orbicular, mostly broader than long, the larger 0.8–1.3 cm. long when fully spread out, definitely shorter than the inner sepals ..... 1. *P. Brownii*

Stems 3.5–7.5 dm. high, bearing 7–12 leaves; leaves green, not glaucous, their primary divisions cuneate at the base, often sessile, the ultimate lobes lanceolate or narrowly elliptic; petals elliptic, longer than broad when fully spread out, the larger 1.5–2.5 cm. long, slightly longer than the inner sepals ..... 2. *P. californica*

1. Paeonia Brownii Dougl. ex Hook. Fl. Bor. Am. 1: 27. 1829; Torr. & Gray, Fl. N. Am. 1: 41. 1838. Illustrations: Bot. Reg. 25, t. 30. 1839; Journ. Royal Hort. Soc. Lond. 12: 433. fig. 24, 1890. (pl. XXXVII, figs. f–n.)

Northern California, from Santa Clara and Tuolumne counties north to British Columbia, east to Wyoming. In California mostly at altitudes of 3000 to 6000 feet. (900 to 1800 meters). The following specimens in the herbarium of the University of California (UC) and in the Dudley Herbarium, Stanford University (DS), are typical. Idaho: Silver City, Owyhee County, *Macbride 943* (UC, DS). Washington: Swauk Creek, Wenatchee Mts., *Quick 1042, 1054* (UC). Oregon: Rock Creek, Morrow County, alt. 1040 m., *Leiberg 95* (UC). California: Quartz Valley, Siskiyou County, Butler *1229* (UC, DS); Jameson Creek, Plumas County, *Hall 9307* (UC); Bartlett Mt., Lake

County, *Abrams 12416* (DS); Mount Hamilton, Santa Clara County, *H. K. Sharsmith 3947* (UC).

The exact eastern limits of *Paeonia Brownii* are uncertain. Rydberg (Rocky Mt. Flora, p. 315) includes Utah in the range; Tidestrom (Fl. Utah and Nevada, p. 202) questions its occurrence there but includes Alberta, which Rydberg does not. In answer to requests by the writer, Dr. Ellsworth P. Killip of the United States National Herbarium (US), Mr. C. A. Weatherby of Gray Herbarium (G) and Dr. H. A. Gleason of the New York Botanical Garden (NY), have examined the material of this species in their collections and report no specimens of *P. Brownii* from either Utah or Alberta. One collection is reported from Wyoming: Jackson's Hole, Lincoln County, *Payson & Payson 2196* (G, NY).

2. Paeonia californica Nutt. ex Torr. & Gray, Fl. N. Am. 1: 41. 1838. Greene, Garden and Forest 3: 356. 1890. (*P. Brownii* var. *californica* Lynch. Journ. Royal Hort. Soc. Lond. 12: 433. 1890). Illustrations: Lynch. l.c. fig. 25, leaf; Parsons, Wild Fl. Calif. 341. 1897; Davidson, California Plants in their Homes, fig. 31, 1898; Armstrong, Field Book West. Wild Fl. 139. 1915; Pickwell et al., Spring Wild Flowers of the Open Field, Western Nature Study 2: fig. 31. 1931; Munz, Man. S. Cal. Bot. 170, fig. 76, 1935; Thurston, Wild Fl. So. Cal. 326, fig. 511, 1936. (pl. XXXVII, figs. a–e.)

Southern and south central California, from Monterey to San Diego County, from sea level to 4000 feet (1212 meters) (*fide* Munz, 1935). The following specimens are typical. California: east of Bryson, Monterey County, *Ferris 8450* (UC, DS); Santa Ynez Mts., Santa Barbara County, *Elmer 3786* (UC, DS); Santa Monica Mts., Los Angeles County, alt. 425 m., *Clokey & Templeton 4447* (UC); San Bernardino Valley, San Bernardino County, alt. 360—400 m., *Parish 6820, 11713* (UC); Encinitas, San Diego County, *Brandegee* in 1884 (UC).

As will be seen from the table, most of the differences between the two species are associated with the greater luxuriance of growth in *Paeonia californica.* This species is larger and better developed in all of its parts than *P. Brownii,* except that no significant differences between the two could be found in the outer sepals, the carpels at anthesis, the mature follicles, and the seeds. *Paeonia californica,* judging from its range, is not hardy, and is a mesophyte. Although the climate of its habitat is semiarid so far as the season as a whole is concerned, *P. californica* completes its active growth during the rainy season, when the ground is more or less moist, and lies dormant during the dry season, depending on food stored in its thick roots. Its leaves and stems wilt very readily.

*Paeonia Brownii,* on the other hand, is definitely hardy, since its shoots sometimes push their way up through banks of snow. It is also semi-xerophytic; at least the latter part of its seasonal growth takes place after precipitation has almost or entirely

ceased, and the ground has become quite dry. Its fleshy leaves retain their turgor for many hours after the stem is broken.

On the basis of these facts, the question arises as to whether or not the differences between *Paeonia Brownii* and *P. californica* are due to the direct stimulus of the environment, and whether they could be transformed one into the other by transplanting. The critical experiments to test this point have not yet been performed, but all available evidence indicates that such transformation would not take place. Many experimenters, notably Turesson (9), have shown that the large majority of adaptations to different habitats within the same or closely related species are genetically conditioned.

Within each of these two species of *Paeonia* variation in the characters by which they differ from each other is not noticeably correlated with differences in habitat. Plants of *P. californica* in Monterey County, central California, are practically indistinguishable from those of the same species occurring about San Diego, 350 miles farther south, which receive about half as much rainfall. Those of *P. Brownii* growing in central California, on Mount Hamilton, are very similar to those found in the Wenatchee Mountains of Washington, 750 miles to the north. Furthermore, *P. Brownii* shows evident "conservatism" in the southern part of its range. It is rare in the Coast Ranges of California and is apparently retreating with the advent of a warmer climate. Many of the plants in the Mount Hamilton colony, the southernmost known locality, produce only small, abortive buds and no flowers, an indication that the species is there dying out. All evidence points to the assumption that plants of *P. Brownii* are not only unable to adapt themselves to a warmer climate, but in addition that they cannot, either by segregation or by mutation, produce offspring that can tolerate a warmer climate. *Paeonia californica,* on the other hand, shows every sign of advancing with the increasing warmth of the climate. It is a rather common plant in suitable spots up to the northern limit of its range, and at its northernmost known station is abundant and very luxuriant. It has not, however, been able to colonize the localities within its range which have a climate corresponding to that required by *P. Brownii.* In the higher mountains of southern California, which have a climate and flora similar to that of the northern Sierra Nevada where *P. Brownii* is abundant, there is no *Paeonia* at all. At present, therefore, all evidence warrants the assumption that neither by physiological nor by genetical change can either of these species become transformed into the other.

Another possible explanation is that the two forms represent geographic variations—varieties, subspecies, or ecotypes (Turesson, 10) of a single species. The crucial test of this, hybridization of the two, would be a long-time proposition since most species of *Paeonia* do not flower until they are four or five years

old. Furthermore, the significance of hybridization tests would be complicated by the fact that both species normally have 60 to 70 per cent of pollen sterility, due to their anomalous cytological condition (Stebbins and Ellerton, in press). At present, however, the facts that no intermediates exist and that hybrids could not be produced except under highly artificial conditions of cultivation, speak strongly in favor of maintaining *Paeonia Brownii* and *P. californica* as distinct species.

*Paeonia californica* is a relatively constant species. Within *P. Brownii,* on the other hand, there is a considerable range of variation, particularly in the amount of dissection of the leaves and in the shape of the segments. In the northern Sierra Nevada a form occurs with leaves much dissected, and frequently with smaller flowers than are typical for the species. Since, however, plants with leaves and flowers of the normal type occur within the range of this Sierran variant, the writer does not consider it well enough marked for recognition as a distinct variety or subspecies.

The phylogenetic relationship between the two species is best determined by comparing them with the Old World species of *Paeonia. Paeonia Brownii* and *P. californica* constitute a distinct subgenus, *Onaepia* (Lynch, 5), which is characterized by small petals; a very prominent disk, usually divided into separate segments; and cylindrical rather than ovoid seeds. The Eurasian species are segregated into two subgenera, *Moutan* comprising the shrubby, and *Paeon,* the herbaceous species. In spite of the shrubby habit, *Moutan* is nearer to *Onaepia* than is *Paeon.* The "tree peonies" of China have, like the American species, a very prominent disk, and both have large seeds with dull coarsely rugose surfaces; the seeds of *Paeon* are smaller, relatively smooth, and often shining. Furthermore, one of the two species of subgenus *Moutan, P. Delavayi* Franch. of southwestern China, has petals almost as small as those of *P. californica,* and in the typical form of *P. Delavayi* they are of a similar reddish color. *Paeonia Delavayi* resembles *P. californica* also in its sepals and carpels and in the shape of its leaves, although those of the Chinese species are much larger and more dissected. In some specimens of *P. californica* the disk segments are relatively thin and are partly fused with each other, recalling the conspicuous, continuous disk of *P. Delavayi.* Both species are characterized by rather indefinite branching, the branches generally bearing well developed leaves as well as a terminal flower bud. In all other species of *Paeonia* (except occasional luxuriant individuals of *P. Brownii*), the side branches bear only a terminal bud, with sometimes a reduced leaf below it. Since *P. Delavayi* must be considered the most primitive species of *Paeonia* extant, (Stebbins, 7) the line which gave rise to *P. californica* and *P. Brownii* must have branched off from the rest of the genus very early in its history.

The fact that the closest connection between the Old and the New World species of *Paeonia* is through species endemic to such remote and different regions as southern California and southwestern China suggests that this connection is very ancient. The Old World species, *P. albiflora* Pall. of Manchuria, from which the well known cultivated peony is derived, is geographically nearest to *P. Brownii* and occupies a somewhat similar habitat, but it is obviously very remotely related to both *P. Brownii* and *P. californica.* In all of the most important morphological characters by which *P. Brownii* differs from *P. californica,* it diverges also from all of the Old World species. In shape and texture of leaves, shape and color of petals, and in habit *P. Brownii* is quite unique. It represents, therefore, an offshoot which has diverged more in morphological characters from the common ancestor of the American peonies than has *P. californica.* The latter species, however, shows more ecological divergence from other species of the genus, since it is the only peony that is not frost-hardy. The most likely hypothesis as to the course of evolution of the two species is that their common ancestor was mesophytic and frost-hardy, as are all Old World species, and resembled morphologically *P. Delavayi* and *P. californica.* This ancestor probably was present in California in Mesozoic or early Tertiary time, and gave rise to a considerable number of ecological and morphological types. Of these all that were mesophytic and frost-hardy perished when the climate of California became warmer and more arid. *Paeonia californica* persisted in southern California by evolving a change in its period of dormancy from the cold winter to the dry summer, but retained most of the morphological characters of its original ancestor. *Paeonia Brownii,* on the other hand, retained its frost-hardiness and winter period of dormancy, but became adapted to dry summers by evolving a series of morphological specializations. Both species, therefore, are derived types, but morphologically *P. californica* is undoubtedly the more primitive.

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### Explanation of the Figures. Plate XXXVII

Figs. *a–e, Paeonia californica* (Santa Ynez Valley, California, *Stebbins 2090*): *a,* terminal primary segment of median cauline leaf, × ½; *b,* the three innermost sepals, × 1; *c,* the largest and smallest petals, × 1; *d,* two stamens, × 1; *e,* disk and follicles at anthesis, × 1.

Figs. *f–i, Paeonia Brownii* (Wenatchee Mts., Washington, *Quick 1042*): *f,* terminal primary segment of median cauline leaf, × ½; *g,* the largest petal, × 1; *h,* two stamens, × 1; *i,* disk and follicles at anthesis, × 1.

Figs. *j–n, Paeonia Brownii* (Sierra County, California, *Stebbins & Jenkins 2157*): *j,* terminal primary segment of median cauline leaf, × ½; *k,* the five innermost sepals, × 1; *l,* the largest and smallest petal, × 1; *m,* two stamens, × 1; *n,* disk and follicles, × 1.

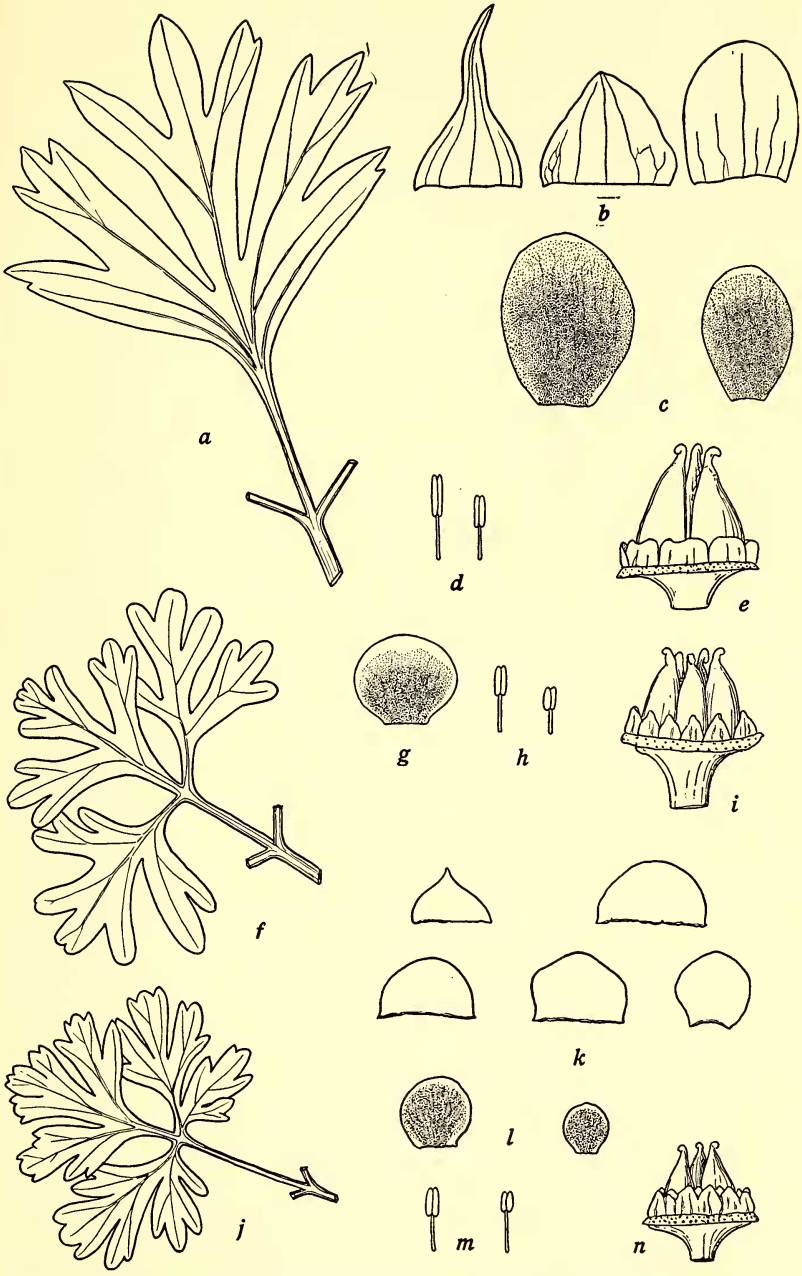


PLATE XXXVII. WESTERN AMERICAN SPECIES OF PAEONIA.

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## HANGING GARDENS OF THE CANARY ISLAND DATE PALM

Ira L. Wiggins

The practice of trimming the older leaves from the trunks of palms used in ornamental plantings provides a temporary arboreal habitat for a number of plants that normally grow only on the ground. The row of Canary Island date palms on either side of Palm Drive on the campus of Stanford University, California, annually supports a total population of many hundred individual plants and a surprisingly large number of species. The relationships between these plants that are normally ground-dwellers and their arboreal supporters, the fluctuations in the "hanging gardens" from year to year, and the variations in the tenacity of such wanderers marooned above their normal sphere are sources of considerable interest.

Many palms growing under wild conditions retain their leaves over a period of years, thus forming a close thatch that shades out any seedlings that may, upon rare occasions, begin growth on their trunks. But even in such trees, the functional leaves, extending upward at sharp angles, provide catchment basins in the bases of their petioles for decaying organic matter and a small quantity of dust. In cultivated trees a considerable portion of this material remains in the fissures between the basal parts of the petioles after the bulk of the leaves has been pruned from the trunk. The functional leaves above form a natural drainage system that directs much of the intercepted rainwater into the basal parts of the petioles. Some of this water is retained in the cups formed by the petiolar bases, some of it trickles over the rims to enter those below and fill the lower reservoirs. Thus, during the course of a heavy rain the entire trunk of one